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by

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THE IMPACT OF CLIMATE CHANGE ON THE PHENOLOGY OF SHORT- AND LONG-DISTANCE MIGRATORY BIRDS

by

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ABSTRACT

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Quickly changing temperatures due to climate change are expected to have devastating consequences on the migratory bird populations around the globe. However, surprisingly, several studies have demonstrated that some species may be able to keep up with the unusually rapid changing temperatures that we are experiencing, as a variety of species in these studies have shown changes in their migratory behavior in response to these changing temperatures. This thesis aims to determine how climate change will affect the migratory behavior in birds and which bird species will be more resilient to these changes. It was hypothesized that short-distance migrants would be more resilient and better able to adapt to climate change than long-distance migrants, and that short-distance migrants would shorten their migratory journey or become residents on their breeding grounds. Two case studies were investigated to determine whether this hypothesis was valid: case study #1 examined the shifts in bird migration timing of long- and short-distance migrants, and case study #2 explored the selection for lower migratory activity and residency in previously migratory bird populations. It was found that short- and long-distance migrants are both responding significantly to the changing temperatures and are adjusting their migration times accordingly. In short-distance migrant populations, it was found that the increased global temperatures are currently favouring birds that are expressing reduced migratory activity. These results suggest that phenotypic plasticity and/or microevolution are at play. It has been concluded that it is still more likely that short-distance migrants are more resilient to climate change than long-distance migrants in the long-run because they show more genetic variability in their phenotypic responses, which means that they have a greater evolutionary potential than long-distance migrants.

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1.0 INTRODUCTION

The evolution of migration in birds is a widely debated subject to this day among ornithologists (Salewski and Bruderer 2007). Over the years, two main theories for the origin of bird migration have been discussed: the "northern-home-theory," which assumes that birds originated from the current northern temperate zone and had to migrate south for their non-breeding activities as the climate changed and the "southern-home-theory," which assumes that birds originated from the tropics and migrated north for better breeding opportunities (Cox 1968; Salewski and Bruderer 2007).

The leading theory is that the ancestors of tropical birds dispersed northward from their tropical breeding sites, supporting the "southern-home-theory" (Cornell University 2007). In the tropics, there is high competition for food and space, as well as high nest predation rates during the breeding season (Mayntz 2019). Birds that migrate out of tropical areas have an advantage over those that do not because they get to utilize the seasonally abundant food and unlimited space in the north, which confers higher reproductive success (Mayntz 2019).

The routes of migrating birds vary widely between different species because migratory behavior has evolved independently (Meunier et al. 2008). Some migratory bird species can be found travelling short distances, within their climate zone, while others travel incredibly long distances, between climate zones (Allaby and Park 2013). Cyclical control mechanisms that stimulate and terminate migration at certain times of the year varies between these different groups of migrants (Meunier et al. 2008). Generally, short-distance migrants use external cues such as environmental variables and photoperiodism to time their migration, while long-distance migrants mostly rely on internal (endogenous) cues such as zugunruhe, a migratory restlessness that triggers the onset of migration from their wintering grounds (Meunier et al. 2008). Some species travelling longer distances are also known to take advantage of photoperiod during their passage to the breeding grounds and/or as a trigger for the onset of homeland migration (Åkesson 2017).

It is important to conserve the migratory bird populations, as they provide vital ecosystem benefits including pest control, the pollination of plants, and seed dispersal (USGS n.d.; Food and Agriculture Organization of the United Nations 2017). They also serve as an important part of the food chain (USGS n.d.). However, the conservation of these birds may become difficult as global climate change continues to take effect and temperatures rise to higher levels (McCarty 2002). Climate change is beginning to affect some bird species' in their behavior, ranges and population dynamics (Nature Canada n.d.). Ornithologists have already noticed changes in the timing of their migration or reproduction, and shifts in their migratory routes (National Audubon Society n.d.). Higher rates of decline in long-distance migratory bird populations compared to those of their short-distance migratory and resident counterparts has also been observed (Howard et al. 2018). Migrating birds are particularly vulnerable to climate change effects because they depend on a range of multiple environments to survive, which may eventually be lost (Nature Canada n.d.). In the past, species were able to respond to global temperature shifts because these shifts were gradual (National Audubon Society n.d.). However, the rate of temperature increase today is 10 times faster than the average rate of increase since the last ice age (National Audubon Society n.d.; NASA 2010). This is a reason for concern because species may not be able to adapt quickly enough to avoid extinction over the next century (National Audubon Society n.d.). Unless serious actions are taken towards preventing global climate change, then a large numbers of bird species will be at risk of extinction (Nature Canada n.d.).

1.1 Objective:

The purpose of this thesis is to identify how climate change will generally affect the migratory behavior in birds and what this means for the migratory bird population. By examining migrating distances, spring arrival dates, fall departure dates, and the proportion of partial migrants in migratory populations, we can predict the potential consequences that climate change will have on migratory species as well as determine which species are more likely to be resilient to these consequences.

1.2 Hypothesis:

It is hypothesized that short-distance migrants will be more resilient and better able to adapt to future climate conditions than long-distance migrants and that short-distance migrants will shorten their migratory routes or become residents in their breeding areas.

2.0 LITERATURE REVIEW

2.1. MICROEVOLUTION OR PHENOTYPIC PLASTICITY

Microevolution and phenotypic plasticity are possible mechanisms than may explain the adaptation of migratory activity to climate change (Charmantier et al. 2008; Schaefer et al. 2008). Phenotypic plasticity occurs when an organism is able to express different phenotypes in response to different environmental conditions (Gienapp et al. 2007; Schaefer et al. 2008), and microevolution is a response to natural selection and involves a change to the genetic constitution of a population over time (Merilä et al. 2001). While a microevolutionary response to climate change could take a few generations, phenotypic plasticity allows individuals to respond to change within their lifetimes (Boutin and Lane 2014). Furthermore, the rapid increase in global temperatures is calling for an increased demand for rapid adaptation, which will mostly occur through plastic changes (Charmantier et al. 2008). Phenotypic plasticity is often highly adaptive (Gienapp et al. 2007) and may even have evolutionary potential (Boutin and Lane 2014; Grant and Grant 2002; Pulido and Berthold 2010). However, an evolutionary response will most likely only occur if a particular trait is already heritable, *e.g.*, the timing of spring migration (Gienapp et al. 2007). Microevolutionary and/or plastic changes are characterized by the shortening of migration distances, shifts in spring arrival and fall departure dates, and the proportion of partial migrants and residents in a previously migratory population (Pulido 2007). In addition, short and long-distance migratory birds will differ in the degree of phenotypic plasticity they express (Charmantier et al. 2008).

2.2 BIRD MIGRATION TIMING

The rapidly changing environment is expected to affect migratory behavior in birds. However, not all changes in migratory behavior are caused by warming temperatures, as some species, such as certain Blackcap (*Sylvia atricapilla*) populations in England, have been altering their migration times in accordance with humans feeding them in the winter (Carey 2009). For the large majority of cases though, phenological shifts are most impacted by warming temperatures. Several recent studies have linked the advanced spring arrival and delayed autumn departure dates directly to climate change, where the maximum temperature has the most influence on the number of days spent at breeding grounds (Butler 2003; Zaifman et al. 2017; Žalakevičius 1998). These studies have all proposed that short-distance migrants are altering their migration patterns more often, and to a greater degree, than long-distance migrants.

2.2.1 SPRING MIGRATION

The timing of spring migration in birds has evolved to match peak food availability (Both et al. 2010; Carey 2009; Jonzen et al. 2006). However, climate change has caused different phenological responses across the trophic levels, making it difficult for migrating birds to breed at the time of maximum food abundance (Both et al. 2006). Mismatching occurs to species that have not yet advanced their spring arrival dates to the time of high food abundance, which could result in reduced availability of food during the feeding of nestlings (Carey 2009). As a consequence, many birds will face declining populations if they are not able to compensate for the advancement of their main food supply (Both and Visser 2001).

To thoroughly analyze the effects of climate warming on spring arrival dates, researchers have examined decades worth of spring sightings data with hundreds of different bird species. These studies have found that short-distance migrants are arriving considerably earlier to their breeding sites than the long-distance migrants (Both and Visser 2001; Butler 2003; Møller 2008; Murphy-Klassen et al. 2005; Pulido and Widmer 2009). In general, species that migrate from nearby temperate areas tend to arrive to their breeding grounds earlier than species that migrate from tropical areas because they are able to adjust the timing of their migration in response to local climate change (Jonzen 2006; Murphy-Klassen et al. 2005; Usui 2017). Tropical-wintering long distance migrants may have more difficulty adjusting to these changes because they time their migration through endogenously driven circannual rhythms, rather than external cues, and thus, they have a lower responsiveness to changing spring temperatures (Both and Visser 2001; Usui 2017). However, contrary to most studies, the research of Jonzen et al. (2006), which was based on long-term banding and observational data in Scandinavia from 1980 to 2004, found that long-distance passerine migrants from the tropics have been advancing their arrival dates more often than short-distance passerine migrants. This suggests that, even though long-distance migratory activity is under endogenous control, individual variation in response to temperature changes during their passage may trigger climate-driven evolutionary changes (Jonzen et al. 2006). In fact, it has been shown that by adjusting migration speed on route, some long-distance migrants have been expressing some degree of variation in their phenotypic response to climate change (Forchhammer et al. 2002; Sparks et al. 2004). However, Both (2007) argued that this variation may just be a result of improved environmental conditions on route, and not an evolutionary response.

2.2.2 AUTUMN MIGRATION

The timing of autumn migration, whether it is advanced or delayed, varies among species (Hällforsa 2020). In some cases, the timing of events on the breeding grounds carry over to affect the timing of autumn migration (Mills 2005; Mitchell 2012; Zaifman et al. 2017). For example, Mills (2005) and Tottrup (2006) both hypothesized that if the amount of time that a species spends on their breeding grounds is constant, and if climate change allows for earlier spring arrival and breeding, than migrants may be stimulated to return to their winter ranges sooner (Filippi-Codaccioni et al. 2010; Mills 2005; Tøttrup et al. 2006). This would support the research of Jonzen et al. (2006) who found that advanced arrival dates in long-distance migrants happened because some long-distance migrants are indeed advancing their annual schedule. Departure from the breeding grounds in autumn is often dictated by the future environmental conditions on their migration home (Åkesson 2017; Rowan 1926). Long-distance migrants rely mostly on circannual rhythms to time their migration; however, at their temperate breeding sites, they are also able to use photoperiod to determine their optimal autumn departure dates (Åkesson 2017). This is how they may be able to shorten their time spent on the breeding grounds, even with no advance in their spring arrival times. Advanced departure dates could be beneficial to a long-distance migrant because they could find better territories if they arrive earlier to their winter homes, which could result in better preparation for spring migration in the next season (Filippi-Codaccioni et al. 2010). Although long-distance migrants have shown some variation in their autumn departure dates, many annual schedules of these migrants have remained unchanged (Butler 2003; Murphy-Klassen et al. 2005). For the majority of cases, long-distance migrants overwintering further away from their breeding grounds are very much constrained by the timing of their migratory journey which prevents adequate adaptation (Both and Visser 2001; Jenni and Kéry 2003).

In contrast, Butler (2003) suggested that short-distance migrants are able to respond more quickly to slightly more favourable conditions than long-distance migrants. Short-distance migrants are likely to delay their autumn migration because the warmer temperatures allow them to benefit from a prolonged breeding season and an increased availability of food later in the year (Hällforsa 2020; Jenni and Kéry 2003). Delayed autumn migration from the breeding site has its disadvantages as well. Mitchell et al. (2012) revealed that late departures could increase an individual's risk of inclement weather during autumn migration and diminished resources at stopover sites as a result of resource suppression by earlier migrants.

2.3 TRANSITION FROM MIGRANTS TO PARTIAL-MIGRANTS/RESIDENTS

The evolution of partial migration in some species is currently in progress (Pulido and Berthold 2010; Visser et al. 2009). The advanced arrival in the spring and delayed departure in autumn, as observed in short-distance migrants, may be a direct consequence of birds wintering closer to their breeding grounds where these species are better able to predict the onset of spring at their breeding sites (Visser et al. 2009). This would explain why short-distance migrants show stronger advancements in arrival dates and longer delays in departure dates relative to long-distance migrants, who often have less flexible migration strategies (Visser et al. 2009). Long-distance migrants may not be able to shorten their migratory journey because they are constrained by the loss of suitable habitat between their breeding and wintering areas (Barbet-Massin et al. 2009). This loss in habitat is predicted to increase with climate change and will cause longer migration distances for these migrants (Barbet-Massin et al. 2009; Doswald et al. 2009), again preventing adaptation (Pulido and Berthold 2010). Selection for lower migratory activity in response to global warming will eventually drive the evolution for residency in short-distant and partial-migratory populations, without the need for "residency genes" by mutation or gene flow (Pulido and Berthold 2010). An increase in the number of resident populations in a number of short-distance migrants has been recently documented in North America and Europe (La Sorte and Thompson III 2007; Pulido and Berthold 2010; Visser et al. 2009). Former migrants would be able to capitalize on reduced migration costs and rapid adjustments to the shifts in timing of the availability of food if they become residents on their breeding grounds (Pulido and Berthold 2010).

2.4 NORTH AMERICAN BIRD SPECIES MOST LIKELY TO CHANGE MIGRATION PATTERNS DUE TO CLIMATE CHANGE

Prior studies have shown how some species will be more adaptable amidst climate change than others. Because adaptability results from phenotypic plasticity, species that are more 'plastic' will naturally be more flexible to changes in their environment. Certain traits may be more plastic than others, and the species that carry these traits are more likely to be favoured by natural selection as temperatures continue to change (Gienapp et al. 2007). Some North American species that have shown these plastic changes in previous studies are highlighted in Table 1. These migrating birds have shown significant changes in their migration timing due to climate change.

Table 1. Changes in bird migration patterns from previous studies.

Study	Location	Species	Type of migrant
Mills (2005)	Ontario	Hermit Thrush (*Catharus guttatus*)	Short-distance
Mills (2005)	Ontario	Magnolia Warbler (*Setophaga magnolia*)	Long-distance
Mills (2005)	Ontario	White-throated Sparrow (*Zonotrichia albicollis*)	Short-distance
Mills (2005)	Ontario	Yellow Warbler (*Setophaga petechia*)	Long-distance
Mills (2005)	Ontario	Yellow-rumped Warbler (*Setophaga coronata*)	Short-distance
Murphy-Klassen et al. (2005)	Manitoba	Common Grackle (*Quiscalus quiscula*)	Partial migrant
Murphy-Klassen et al. (2005)	Manitoba	Killdeer (*Charadrius vociferus*)	Partial migrant
Murphy-Klassen et al. (2005)	Manitoba	Wilson's Snipe (*Gallinago delicata*)	Long-distance
Murphy-Klassen et al. (2005)	Manitoba	Canada Goose (*Branta canadensis*)	Short-distance
Murphy-Klassen et al. (2005)	Manitoba	Hooded Merganser (*Lophodytes cucullatus*)	Short-distance

Butler (2003)	New York	White-throated Sparrow (*Zonotrichia albicollis*)	Short-distance
Butler (2003)	New York	Brown-headed Cowbird (*Molothrus ater*)	Short-distance
Butler (2003)	New York	Eastern Bluebird (*Sialia sialis*)	Partial migrant
Butler (2003)	New York	Purple Martin (*Progne subis*)	Long-distance
Butler (2003)	New York	Field Sparrow (*Spizella pusilla*)	Short-distance

Some of the common species mentioned in Table 1 are presented as photos in Figure 1; this includes one long-distance migrant (Purple Martin), one short-distance migrant (White-throated Sparrow), and one partial migrant (Common Grackle).

Figure 1. White-throated Sparrow (Cornell University 2019) (top left), Common Grackle (Dunne 2019) (bottom left), and Purple Martin (Horn 2005) (right).

3.0 RESULTS

3.1 CASE STUDY #1: SHIFTS IN BIRD MIGRATION TIMING OF LONG-DISTANCE AND SHORT-DISTANCE MIGRANTS

As climate change has progressed, alterations in migration strategies in birds have become a widely studied phenomenon; however, the extent of these alterations has only recently begun to be analyzed (Zaifman et al. 2017). Utilizing data from the citizen-science website eBird and historical temperature data, Zaifman et al. (2017) analyzed bird migration patterns to determine differences in their correlation with historical temperature changes. In this study, bird migration timing was measured annually from 2010 to 2016 in two states warming quickly (Alaska and Maine) and one state warming gradually (South Carolina). Bird species in each state were manually categorized into year-round residents, summer residents, winter residents, and transient migrants. The birds were then further categorized into long- and short-distance migrants based on whether they travelled more than ~2000 km (long-distance migrants) or less than ~2000 km (short-distance migrants) between breeding and wintering grounds.

Figure 2 shows the general alterations that were found by Zaifman et al. (2017) in bird migration timing by state. It also demonstrates the differences between the long-distance and short-distance migrants showing changes in migration patterns due to changing temperatures.

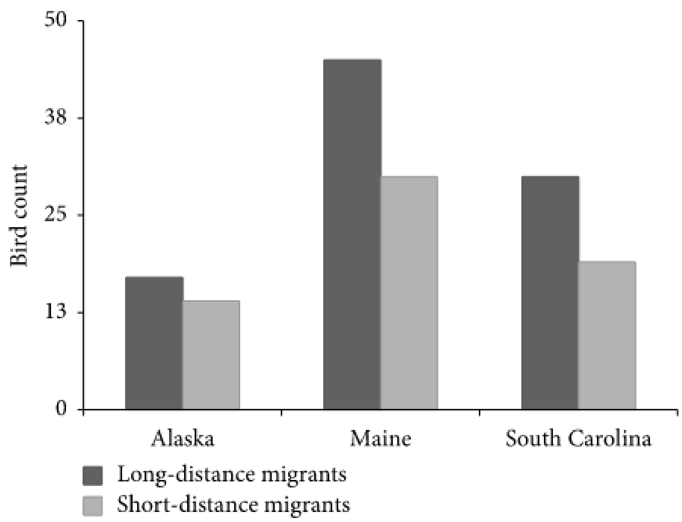

Figure 2. The long- and short-distance migrant species that showed changes in migration patterns over time from 2010 to 2016 in Alaska, Maine, and South Carolina (Zaifman et al. 2017).

It was determined that each state contained species that showed shifts in the timing of their migration, and these shifts correlated with the warming temperatures from 2010 to 2016. In each state, over half of the birds that had altered their migration timing were long-distance migrants. One long-distance migrant that had adjusted its migration patterns during the span of this study was the Semipalmated sandpiper

(*Calidris pusilla*). As the minimum temperature in Maine increased, this species remained in the same area of Maine for a longer time.

A feature selection and analysis were performed on summer resident, winter resident, transient spring, and transient fall birds to determine the features most associated with changes in bird migration timing. For each dataset in their research, five features were ranked (state, migration distance (long or short), and maximum, minimum, and mean temperature) in accordance with changes in the migration pattern at arrival date, departure date, and duration of stay. Table 2 shows the analysis of the selected 'most influential' feature impacting changing arrival dates, departure dates, and number of days for summer resident, winter resident, and transient spring and fall migrations.

Table 2. The most influential features that impacted the changing arrival dates, departure dates, and number of days stayed for the spring and fall migrations of summer resident (SR), winter resident (WR), and transient (T) species (Zaifman et al. 2017).

	Most important feature			
	SR	WR	T spring	T fall
AD	State	Min temp.	State	State
DD	Mean temp.	Max temp.	State	State
ND	State	Max temp.	Max temp.	Max temp.

In this case, summer residents refer to those species that have travelled north to their summer breeding grounds. Winter residents refer to those that have migrated back south from their summer breeding grounds to their wintering locations. Transient migrants are the migratory species that do not nest or winter in the area where the data was collected for the study but use the area as a stop-over site on route to or from their summer or wintering grounds.

The arrival dates of summer resident and transient bird changes were most influenced by state. The most important feature for the departure date of summer residents from their breeding grounds was mean temperature. The maximum temperature at the stop-over site was the most important feature for the number of days stayed at stop-over sites in transient migrants. During winter resident migration, the minimum temperature was the most important feature for the arrival date to their wintering grounds. In contrast, the maximum temperature most influenced their departure date and length of stay.

3.2 CASE STUDY #2: CURRENT SELECTION FOR LOWER MIGRATORY ACTIVITY WILL DRIVE THE EVOLUTION OF RESIDENCY IN A MIGRATORY BIRD POPULATION

As temperatures continue to increase, the survival and adaptability of many species will be tested. Pulido and Berthold's (2010) aimed to predict how certain species will adapt to the sudden and rapid increase in temperatures. This was accomplished through examining the migration behavior in a population of European Blackcaps (*Sylvia atricapilla*) (Figure 3) to test for evolutionary responses to recent climate change. The Blackcap is a small passerine bird that typically breeds in southern Germany or Austria and winters in southern Europe to northern Africa or the United Kingdom (Figure 3).

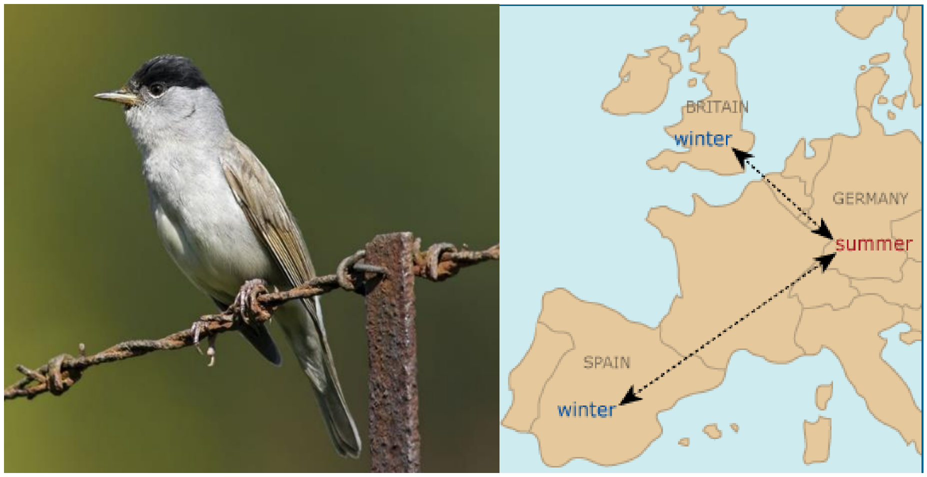

Figure 3. Blackcap (left) and its migratory route in Europe (right) (Britannica 2021; Understanding Evolution 2010).

This species is partially migratory, which means that its population consists of both migrants and residents. The Blackcap, in particular, exhibits a wide variety of migration patterns, with some travelling short distances, some travelling long distances, and some who do not migrate at all (Delmore et al. 2020). Specifically, Pulido and Berthold (2010) used Blackcaps in their experiment because they have strongly responded to recent increases in temperature and associated environmental changes in central Europe, making them the model species for studying the genetics and evolution of avian migration.

Using a common garden experiment and selective breeding in captivity, as well as an artificial selection experiment, Pulido and Berthold (2010) were able to collect the relevant data to test whether Blackcaps have adapted their migratory behavior to the recent increase in ambient temperatures and to the resulting widening of the reproductive time window.

Experiment #1: Common Garden Experiment. The common garden experiment allowed Pulido and Berthold (2010) to draw inferences about genetic changes in wild populations with a strict and controlled set of experimental conditions that did not change over time. This was achieved through collecting nestlings at an early age, hand-raising them, and studying them in climate-controlled chambers in captivity from 1988 to 2002. These results showed a genetic reduction in migratory activity, which were not induced by environmental conditions or maternal effects (environment provided by mothers to offspring) from the parents collected in the wild. All traits investigated showed moderate to high heritabilities. A change in the response of the age at onset of migration to hatching date was also found within the 14 years of this study.

Experiment #2: Selection Experiment. Between 1996 and 2002, Pulido and Berthold (2010) conducted an artificial selection experiment in which a total of 305 Blackcaps were bred using the birds collected in the wild from 1995 and 2001. Lower migratory activity was selected for in a selection line, which they ran for up to five generations. The response of the amount of migratory activity was highest in the first generation of selection and decreased thereafter. Overall, the selection experiment showed strong responses to the selection for lower migratory activity, yielding a total of 14 non-migratory individuals (individuals showing no migratory activity) in an exclusively migratory population.

4.0 DISCUSSION

Because of spatial differences in the strength of climate change, bird migration timing is location-specific, with both short- and long-distance migrating birds adjusting their migration timing differently through different latitudes (Rubolini et al. 2007). This phenomenon is best represented through the feature analysis of Zaifman et al. (2017) (Table 2), where the authors attempt to determine why species were altering their migration timing at different rates. In the feature analysis, a migrant's timing changes were most influenced by temperature and state. In Maine and South Carolina, migrants stayed longer at their breeding grounds as temperature increased, while the opposite trend occurred in Alaska. This seems to be a consistent pattern among both short- and long-distance migrants. Based on all of the species studied, Zaifman et al. (2017) also observed that maximum temperature had the most influence on the arrival date, departure date, and the number of days stayed at the breeding grounds (summer resident migration), and that minimum temperature was most associated with the arrival date at the wintering grounds (winter resident migration). These results indicate that birds may migrate to their warmer wintering grounds to avoid the harsh weather conditions in their breeding grounds (Somveille et al. 2015). It also suggests that birds may return to their breeding grounds as the maximum temperature during the winter increases because a temperature increase at the wintering grounds can indicate a temperature increase at the breeding grounds, as well as a larger abundance of food (Barcena et al. 2004).

My thesis hypothesized that short-distance migrants would be better able to adapt to changing climate conditions than long-distance migrants. Based on Zaifman's et al. findings, this statement is may not be entirely accurate. In previous studies, it was often suggested that the ability to change migration patterns through phenotypic plasticity in response to temperature changes is a trait that is selected for only in short-distance migrants (Rubolini 2007; Viser and Both 2005). However, Zaifman et al.

(2017) suggested that long-distance migrants are now adjusting their migration patterns as well and by a significant amount (Figure 1); hence, challenging the conventional idea that species wintering closer to their breeding grounds should respond more strongly to climate change than those long-distance migrants wintering in the tropics. An example of such a long-distance migrant is the Semipalmated Sandpiper. Zaifman et al. (2017) believed that "by shifting its migration pattern, the semipalmated sandpiper may be adjusting to find more advantageous conditions that may allow it to increase population numbers." This further supports the idea that long-distance migrants have some degree of phenotypic plasticity over the timing of their migration.

It is well known that long-distance migrants base their migration timing primarily on circannual rhythms, which are not influenced by outside factors, such as temperature and photoperiod. But long-distance migrant still seems to be changing the timing of their migration somehow. The simplest explanation, argued by multiple sources (Jonzen et al. 2006; Marra et al. 2005; Tøttrup et al. 2008) appears to be that long-distance migrating birds are shifting their migration patterns in response to changes in temperature. Warmer temperatures can indicate a surge in the food supply at the breeding grounds, so migrants will become inclined to alter their migration patterns in response to these warming temperatures to arrive at the breeding grounds at peak food abundance (Barcena et al. 2004). Since long-distance migrants are unable to sense a change of temperature at their breeding areas while wintering in the tropics, the initiation of their migration from the wintering grounds may not vary greatly. However, they may experience this change in temperature as they progressively approach their breeding grounds, allowing them to adjust their migration speed to match the climatic conditions along their passage (Jonzen et al. 2006; Marra et al. 2005; Tøttrup et al. 2008). An increase in the speed of migration may not necessarily mean an increase in acceleration. However, if the weather in the spring becomes warmer, and this causes an earlier peak in food abundance in habitats used as stopover sites, migrants would be able to increase refueling rates and shorten visits at these sites, which would in turn speed up the migratory process (Coppack and Both 2002; Jonzen et al. 2006). This would also optimize their arrival time at the breeding areas while taking advantage of a climate-induced early spring. This theory supports Tøttrup's et al. (2008) that suggests that species migrating longer distances may experience a degree of phenotypic responsiveness to spatial variability in conditions during their journey. Short-distance migrants, on the other hand, are able to adjust the onset of their spring migration in response to the temperature changes on their wintering grounds.

My thesis also hypothesized that short-distance migrants will shorten their migratory routes or become residents in their breeding areas. This is supported by Pulido and Berthold (2010). Their findings provide strong evidence for microevolution being the underlying mechanism for the rapid adaptive changes in migration seen in many Blackcap populations across Europe. Using the common garden experiment, they demonstrated a genetic reduction in migratory activity and an evolutionary change in phenotypic plasticity of migration onset. In the artificial selection experiment, a simulation of the current selection in the wild favoring shorter migration distances was conducted. The results showed that all monitored traits in the experiment had moderate to high heritabilities, suggesting that migratory activity strongly responds to selection in the wild and that this process will eventually lead to the evolution of a partial migrant. If this selection for lower migratory activity continues, residency will rapidly evolve in completely migratory bird populations.

In the wild, the global increase in temperature is currently favouring birds that are wintering closer to their breeding ground, and it is likely that populations of short-distance migrants will strongly respond to these changes in selection (Pulido and Berthold 2010). The advancement and lengthening of the breeding season in Blackcap populations and the increased observations of Blackcaps wintering in southern Germany are examples of such changes in selection (Pulido and Berthold 2010). A reduction in migratory activity may be an important factor in the adaptation of migratory birds to climate change because it reduces migration costs and facilitates rapid adjustments to the shifts in the timing of food maximum food abundance on the breeding grounds to avoid possible mismatching during the breeding season (Pulido and Berthold 2010).

5.0 CONCLUSION

By analyzing recent alterations in the migration phenology of both short- and long-distance migrating birds, this thesis has shown how many of these changes are significantly associated with climate change. There is no doubt that many migrating bird species will fall victim to the effects of climate change; however, it is also important to note that others may be very adaptable and resilient to these changes. Short- and long-distance migrants both include such resilient species that are able to show variation in their behavior in response to environmental changes. Firstly, although previously thought be constrained by their long migration distances, long-distance migrants are responding by adjusting their migration patterns during the migratory process in accordance with environmental temperatures. Secondly, short-distance migrants, such as Blackcaps, have responded by wintering closer to their breeding grounds or becoming non-migrants who permanently reside on their breeding grounds. Recent reports (Bókony et al. 2019; Pulido and Berthold 2010) have found that selection is strongly favouring those birds that exhibit a reduction in migratory activity. If mean migratory activity decreases, the evolution of residency will become inevitable in a previously short-distance migrating population.

While phenotypic plasticity is important in the quick responses to environmental changes and may have adaptive potential, microevolution is the only mechanism that will ensure populations will cope with the very rapid and prolonged shifts of climate change (Gienapp et al. 2007). To discover whether a species is displaying a microevolutionary response to climate change, directional selection and heritability of migration time need to be demonstrated (Gienapp et al. 2007). These evolutionary variables have been expressed in the short-distance migrants studied in this thesis paper. Although long-distance migrants have shown some phenotypic response to recent climatic changes and may still have evolutionary potential, they have not nearly exhibited the amount of genetic variability that short-distance migrants have. To answer the question of which species group will be more resilient to climate change, I believe that short-distance migrants have a stronger lasting chance at the potentially devastating effects of climate change.

6.0 LITERATURE CITED

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